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NOTES UPON THE ANATOMY AND HISTOLOGY OF THE PROSENCEPHALON OF TELEOSTS.

By C. L. Herrick.

Our knowledge of the microscopic structure of the cerebrum of bony fishes is very imperfect, and I shall endeavor to show that, notwithstanding the great progress recently made in determining the difficult homologies involved, gross misconceptions pass current at the present time. The fundamental difficulty lies in the fact that the cortex is anatomically absent though morphologically present. In other words, though there is no functionally normal cortex, its place is taken by an epitheligerous membrane which in all important morphological particulars substitutes for it. It is quite a different question whether the cortex is physiologically represented; i. e., whether cellular structures exist which functionally replace the undeveloped cortical areas. This may rank among the most important question of physiology as it undoubtedly is of morphology. Inasmuch as the cortex of higher vertebrates serves solely as the organ of consciousness in the limited sense, if it could be shown that it is not only anatomically absent, but physiologically unrepresented, we should have strong reason to suppose that consciousness is practically absent in the group of fishes and thus is an unnecessary element in a purely animal existence even of a relatively highly differentiated organism.

On the other hand, if it could be shown that some other cell aggregate functions in place of the suppressed cortex, it might be hoped that in locating the substituting areas we should obtain the clue to the origin of the cortex and the law of development or, rather, the archetectonic plan of formation. In the latter respect we have secured so much concurrent evidence from widely different sources that the case seems comparatively clear.

If the fish brain, in spite of its great dissimilarity to the brains of higher vertebrates is actually homologous with the latter in detail, it should be possible to discover the exact homologies of the separate organs, or determine the absence of certain parts, together with the morphological reasons for their suppression. In this direction nothing was possible before the pallium had been identified with the cortex and the homologies of the ventricles had been determined in conformity therewith. Even since this has been accomplished many homologies remained uncertain which were essential to a proper understanding of the evolution of the brain of higher vertebrates. None of these homologies are more important than those which relate to the commissures which may naturally be taken as the points of reference. In this last mentioned direction a study of the Drum (*Haplodinotus*) has fortunately afforded the necessary clues.

What follows is a brief summary of a detailed paper to appear in the December number of the *Journal of Comparative Neurology*, forming part of a series which has appeared in several previous issues. The methods pursued will be given in full in connection with the paper, so that it is only necessary to say that a modification of the hæmatoxylin process has been hit upon, which serves to sharply differentiate all the histological elements, bringing out the variations in cell-structure beautifully. In fact a fish brain thus treated is histologically, instead of the least satisfactory, rather the most beautiful of brain preparations. A large series of sections has been secured from which a few of the more important data are here noted.

First, in respect to histological differentiation within the cerebrum. If the axial lobe of the fish cerebrum represents functionally the entire brain, as would seem probable unless one claims that the fish leads a purely reflex nervous existence, that there should occur in it the various types of cells which characterize the several regions of the cortex in higher animals. The writer has abundantly shown in a series of publications covering most of the classes of vertebrates that there is a structural difference between the kinesodic and æsthesodic areas of the cortex and that the motor and sensory cells are more distinctly aggregated in lower than in higher vertebrates. In other words, that types of cells, which in higher animals are interblended, are quite distinctly seggregated into definite areas in lower groups. Thus we have shown that in rodents and marsupials the motor and sensory cells are more distinct and topographically separable than in higher animals, that in reptiles they are much more sharply limited than in mammals and that in fishes the distinction is still sharper. Mr. Turner, who at our suggestion investigated the same question in birds, has found a close resemblance to the reptilian type and fully corroborates the statement that complete structural dissimilarity between kinesodic and æsthesodic cells prevail in the Monocondylia. Whether we regard the brain of a fish as the result of a retrograde metamorphosis from a more typical structure, or as representing a primitive condition, it will be conceded that the cells corresponding to kinesodic and æsthesodic processes must be in all probability represented. The absence of the cortex limits our search to the axial lobe. Observations upon various groups of reptiles have led me on several different occasions to suggest that the axial lobe, seen in those groups where the cortex is present, is a sort of proliferating centre from which cortical cells are formed.[1]

This hypothesis has been further substantiated by the observations of Mr. Turner,[2] upon the axial lobe of various birds. It is also worthy of note that the birds resemble fishes in the great restriction of the cortex and in specific substitutions therefore in the form of niduli within the axial lobe. It would, therefore, appear legitimate to consider the axial lobe as the source from which the cortex has sprung, so far as its histological elements are concerned, a suggestion which is further emphasized by the fact, brought out by Professor His and extended by the writer, that all neural elements are derived from the epithelial structures lining the ventricle.

A corollary of this would be the concentration of all commissures and tracts belonging strictly to the cortex in the axial lobe. The position of such structures might then serve to determine the direction in which the complicated brain of higher vertebrates has been folded and differentiated. This principle the writer has employed in the determination of the histogenesis of the cerebellum. (Compare a recent article on the cerebellum in "*Science*.") Now to return to the special subject of our study, the cerebrum of the Drum is moderately large and well differentiated. The pallium is well developed and completely devoid of nerve cells, but the surface of the cerebrum is nevertheless quite conspicuously fissured. It was shown by my brother and myself in a series of articles in the *Journal of Comparative Neurology* for June and October, that the cerebrum of teleosts is more or less constantly marked by fissures which cannot be homologized, except in two cases, with the fissures of higher vertebrates, because of their lying in the surface of the axial lobe rather than the cortex. Nevertheless, these fissures serve to constantly delimit certain areas of the axial lobe, which are also remarkably constant in their histological differentiation. Using these land marks it has proven possible to define a number of distinct lobes, which have received names suggestive of their position. The homologue of the hippocampus, however, is easily recognized, not only by its position, but by reason of the anatomical connections. It forms a raised lip or projection along the ventral surface and is lateral of a fissure perfectly homologous of the rhinalis of higher animals. The forward prolongation may be compared to the convexity in the corresponding region of the pyriform lobe of rodents. Caudad it expands into an obpyriform lobe which is the hippocampus in a restricted sense. Throughout its entire extent, the hippocampal lobe is the part which mediates between the pallium (cortex) and the axial lobe, and is therefore identical in position with the outer part of the hippocampus of mammals. In microscopic structure it differs from the adjacent regions. The radix lateralis, which, as we have shown in the series of articles above referred to, is wholly distinct from the radix mesalis, follows the rhinalis fissure and may be traced in a single horizontal section to the caudo-ventral aspect of the hippocampus, where the fibres spread out upon the surface in a way entirely similar to that observed in rodents. The resemblance to the homologous organ of higher vertebrates does not cease here, but from the deeper parts of the hippocampal lobe an ental tract, corresponding to the hippocampal commissure and descending fornix tract, arises and passes cephalomesad to cross just caudad of the strongly developed callosum. At this point a branch is given off precisely like the fornix which passes to a bilobed cellular mass, projecting ventrad into the ventricle caudad and dorsal of the lamina terminalis. In appearance and structure, as well as fibrous connections, these tubers can only be regarded as identical with the corpus fornicis. Nothing is wanting to make the homology perfect. Fibres from the fornix body can be traced into the thalamus, but nothing indentifiable with the mammillaries could be made out with certainty.

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[1] Notes on the Brain of the Alligator. Journ. Cincinnati Society of Natural History, vol. XII, p. 455; Contributions to the Comparative Morphology of the Central Nervous System, II. Morphology and Histology of the Brain of certain Reptiles, *Journal of Comparative Neurology*, vol. I. p. 21, March 1891.

[2] *Journ. Comp. Neurology. Vol. 1, p. 71.*

The radix mesalis of the olfactory is much larger and more distinct, and seems to be derived from a mass of cells occupying the pes, while the radix lateralis springs from the pero. This bundle passes caudo-dorsad and then mesad and crosses in a special ventral portion of the præcommissura quite distinct from the specific homologue of the latter. In the Drum, the olfactories are attached to the cerebrum, or more strictly, to the præthalamus just at the origin of the lamina terminalis. They are obviously not appendages of the prosencephalon, as we have suggested on morphological grounds it would be impossible for them to be, but the radices have suffered division or latero-flexion with the outgrowth of the secondary cerebral vesicles. The origin of the hippocampal loop of the olfactory tract becomes obvious by inspection of an embryonic brain or that of a fish, it being the least diverted portion of the walls of the primitive prosencephalic ventricle carrying with it the tracts and commissural origins proper to it. It is a curious fact that of the two radices of the olfactory, one belongs to the dorsal and the other to the ventral system and the commissural or decussational fibres likewise belong, one to the ventral the other to the dorsal of the two primary commissural systems of the neural tube. The radix lateralis connects, via hippocampus, with the dorsal system associated with the callosum, *i. e.* the fornix and hippocampal commissure. The radix mesalis, on the other hand connects with the anterior commissure system. It would thus appear that the olfactory system, including the pes, is homodynamous with a complete neuromere or symmetrical fraction thereof.

The corpus callosum has been so much studied of late that it would be an act of presumption to put forth a new theory without the amplest evidence. In the present case the writer, in presenting an interpretation entirely different from the prevailing one, does so with the perfect confidence that any one who will examine the facts exhibited in our sections will be convinced of the correctness of the view. In a previous paper[1] the writer has indicated the existence of a hitherto unsuspected commissure in *Lepidosteus* and identified it as the homologue of the callosum hippocampal commissure in the following words:

" *Commissures of the Cerebrum.*—The exact equivalence of the commissures of the cerebrum is a matter of much difficulty in these fishes where the whole dorsal and median portion of the tectum cerebri or mantle portion is apparently represented by the pallium cerebri. Considering, however, that the direction in which the cerebrum has been differentiated in higher animals is caudad, and that, in the lower brains, bodies which lie caudad or dorsad in higher vertebrates must be sought dorsad or cephalad, it is not difficult to homologize the pallium with the plexus-bearing projection from the posterior and mesal margin of the mantle. Since the plexus in this case occupies the vertex, instead of projecting from the caudal region, all structures morphologically cephalad of the plexus must be sought still further cephalad or ventrad. Using this clue, and observing that the cerebral cortex folds ventrad over the olfactory structure, we think we find a homologue of the calloso-hippocampal commissure connecting the two halves of the cerebrum cephalad of the openings of the olfactory crura into the common ventricle, and lying just entad of the membranous lamina terminalis. The bundle is very small and seems to contain a few fibres from the olfactory regions, as well as others from the cephalic portions of the cerebrum. No indication of the callosum was seen in Scaphirynchus."

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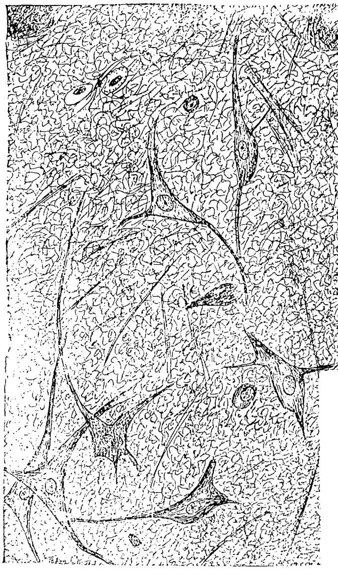
[1] Topography and Histology of the Brain of certain Ganoid Fishes, Journ. Comp. Neurology, vol. I., p. 167–168.

In the Drum, however, the callosum is relatively large and conspicuous. It lies far cephalad and somewhat ventrad (morphologically dorso-cephalad) of the anterior commissure. It is directly associated with a large nidulus of pyramidal cells, which occupies a central position in the axial lobe in the direct line of the pyramid fibres produced. This central lobe is the unmistakable homologue of the motor areas occupying the cephalic cortical regions of higher vertebrates, and is therefore properly associated with the callosum. The callosum lies dorsad of and adjacent to the line where the pallium adheres to the axial lobe. It is therefore just where it would be expected upon the hypothesis that the structures otherwise found in the cortex had been driven from the latter by its conversion into the pallium, or, better, had failed to grow out into the pallium when it was formed.

Remembering that the growth of the cerebrum has been largely dorso-caudad, such a retarding as here supposed would leave the callosum where we find it at the cephalic juncture of pallium and axial lobe. Since the interventricular cortical lobe is suppressed in teleosts, it follows that the callosum and anterior commissure, which are collocated by accident, rather than relationship in Reptilia and Amphibia, are here widely separated. These facts are entirely in agreement with the highly philosophical theory of the commissures proposed by Osborn, though in the present case, Osborn supposed (an opinion in which the writer at first shared) that the callosum of fishes is contained in the anterior commissure group. The considerations above mentioned show that in the absence of the mesal walls of the cortex a collocation the two commissural systems, except by great axial shortening of the brain, would be impossible.

As to the general question, whether it is proper to suppose that the cell structures normally found in the cortex are derived from the axial lobe and may be retained there by conversion of the cortex to a cell-less pallium, I refer, first, to the data of embryology; second, to my own observations upon young

PLATE VIII.



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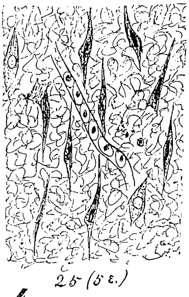

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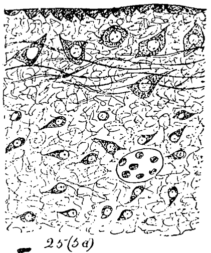

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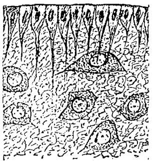

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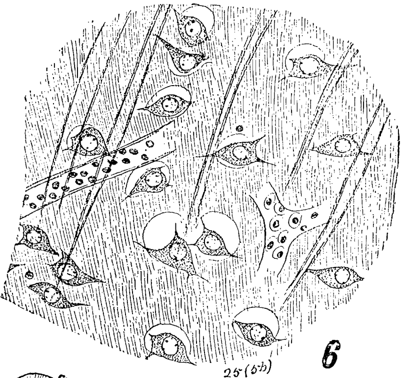

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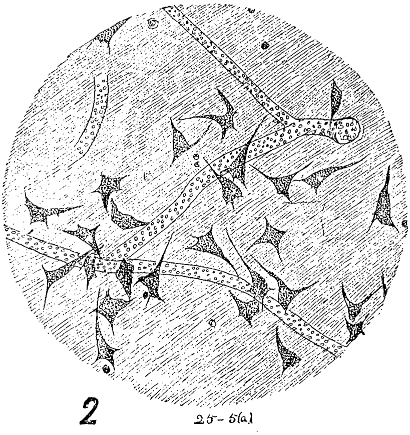

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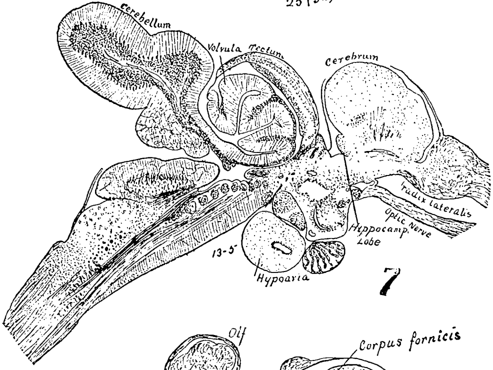

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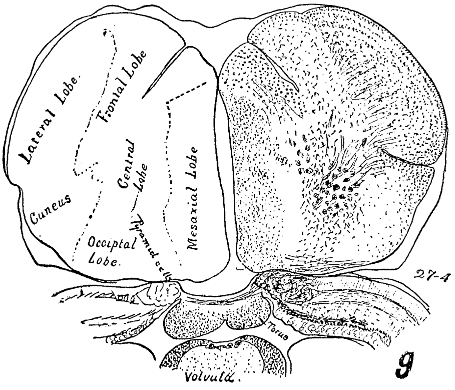

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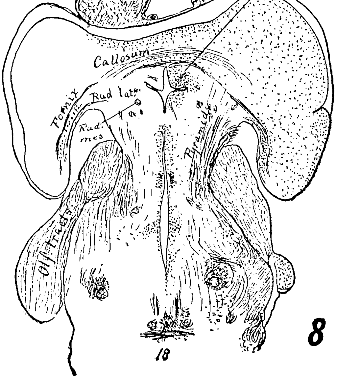

8

Brain of Haploidonotus.

reptilian brains; and, third, to the discovery made by my pupil, Mr. Turner, that in the brain of birds there are several introverted cortical niduli within the axial lobe, in regions where the cortex is restricted or aborted.

In general, then, it seems proper to regard the cerebrum as a product of a dorso-lateral pouch from the thalamus, carrying with it the commissural systems (dorsal and ventral) belonging to what may be called the præthalamic segment or neuromere. The hippocampal system may be regarded as representing a part of the dorsal commissure, the callosum a part of the ventral and perhaps part of the dorsal, while the anterior commissure is decidedly ventral.

At any rate the morphological relations in fishes are precisely as in higher vertebrates. The conclusions above indicated may be thus summarized.

1. Fishes have a distinct corpus callosum separated from and on the opposite side of the ventricle to the præcommissura.
2. Fishes have a distinct fornix and hippocampal commissure.
3. A well-marked fornix body is present in fishes having normal fibre connections.
4. There are distinct radices mesalis and lateralis in the ichthic olfactory lobe, the former crossing in the anterior commissure, the latter passing to a hippocampal lobe.
5. The hippocampus of fishes is a distinct lobe of the axial part of the cerebrum.
6. The axial lobe in fishes is composed not only of the elements proper to the corpus striatum or sauropsidian axial lobe but also contains rudiments of the sensory and motor niduli of the cortex.
7. The two types of cells are sharply differentiated.

EXPLANATION OF PLATES.

PLATE VII.

Horizontal longitudinal sections through the entire brain of the drum, *Haplodinotus grunniens.*

Fig. 1. Section through the olfactory lobes and corpus fornicis. The radix lateralis is easily followed throughout its entire length from the lateral aspect of the pero to the hippocampus. The radix mesalis arises in the pes and, curving ventral and then dorsal, appears cephalo-ventrad of the axial commissure as a circular bundle.

Fig. 2. Section at the level of the axial commissure (decussation of the basal peduncular tracts of Edinger) and callosum.

Fig. 3. Section above the level of the præcommissure, the tracts of which are visible in the section.

Fig. 4. Section near the dorsal surface of the cerebrum. The figure illustrates the structure of volvula and cerebellum.

PLATE VIII.

Fig. 1. Portion of olfactory pero highly magnified.

Fig. 2. Pyramidal (kinesodic) cells from the central lobe of cerebrum.

Fig. 3. Superficial portion of lateral lobe to show epithelium. The æsthesodic cells are transversely cut.

Fig. 4. Cells from E in fig. 3 of the previous plate.

Fig. 5. Portion of the cuneus.

Fig. 6. Cells from the lateral lobe.

Fig. 7. Longitudinal section through the whole brain.

Fig. 8. Horizonal section through entire brain somewhat dorsad of fig. 3 of the preceding plate.

Fig. 9. Section just dorsad of the olfactory crus to show the relations of fornix tracts and callosum.